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The Yellow-wattled Lapwing, *Vanellus malabaricus* (Boddaert), a tropical dry-season nester

II. Additional data on breeding biology

BY

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(*With a plate*)

INTRODUCTION

We have recently published (Jayakar & Spurway 1965) an account of the incubation behaviour of *Vanellus malabaricus* in the large exposed gardens of a residential area of New Capital, Bhubaneswar. This paper continues these observations, and provides provisional answers to some of the questions raised.

The terrain consists of lateritic rock with a thin top-soil recently cleared in order to be covered with relatively large thinly-spaced buildings. These building operations ensure that, in addition to the outdoor taps, which are a feature of India, there are also many temporary sources of water. The average monthly rainfalls in millimetres beginning with January are : 14·5, 23·6, 16·0, 23·4, 67·3, 216·7, 336·8, 320·0, 248·8, 158·0, 53·3, and 4·8.

The observations were primarily made from our house, which is shaded in the present map (see Plate) and shown in part in the map in our previous paper. The map shows an area of about 15 hectares or 37 acres which can be critically surveyed from the roof of this house.

Within this area tarred roads are shown hatched. These are bordered by pavements and/or grass verges. Other roads and lanes are shown by parallel lines. To the north and north-east uneven treeless waste-land extends for over 350 m. In all other directions visibility is abruptly obscured by buildings (not all of which are marked) and their associated hedges and trees. Nests were of course regularly visited, and were also watched from various verandahs of the same house. This area was surveyed on most days from 21/xii/63 usually for over an hour in the evening while a roosting census was being taken.

We have previously discussed the idiosyncracies of wattle and wing coloration by which we distinguish the members of a pair. Similar characters were appreciated in pair 6 but not pairs 5 and 7. The male of pair 6 (again defined as the animal who invariably trod during copulation) walked awkwardly and flew with his right leg dangling.

Once again we thank our neighbour Shri S. K. Ghose for allowing us to watch nest 3′ and the tap, both of which were in his garden.

Breeding Economy

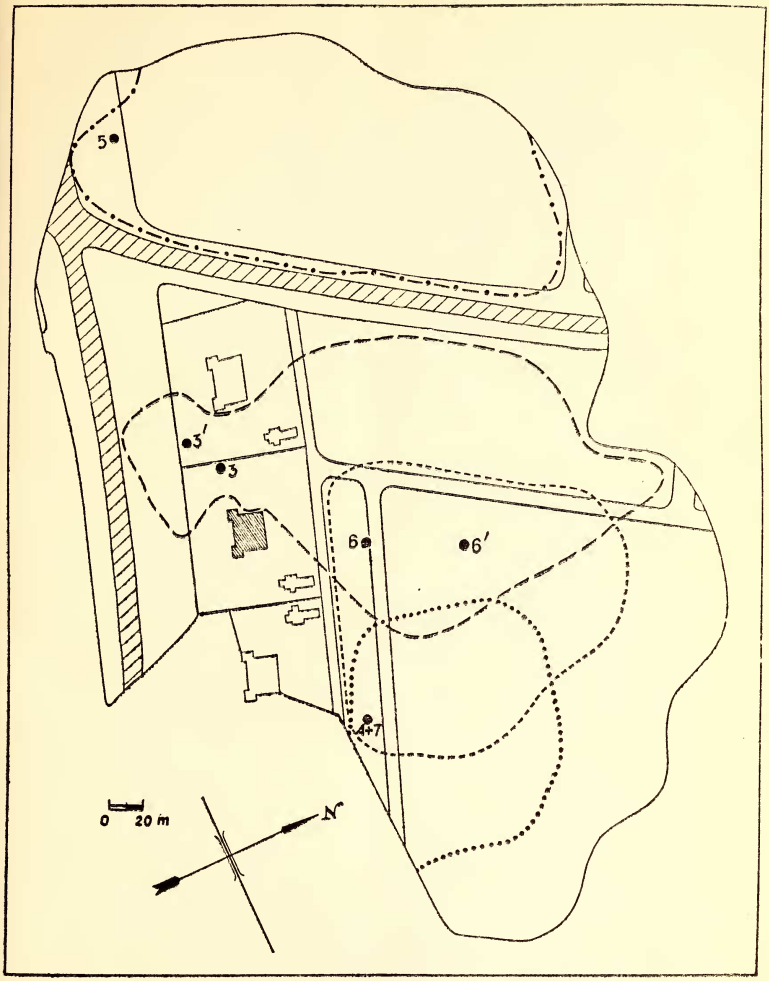
Table I lists some figures for the 7 clutches found during 1964 ; and the location of these and the associated territories are mapped in the Plate.

Table I

Dates of observations made

Clutch	3	4	3′	5	6	7 (perhaps 4″)	6′
0 egg	..	..	..	..	**19/iv**	..	**15/v**
1 egg	..	..	..	..	21/iv	..	21/v
2 eggs					22/iv		22/v
3 eggs			**12/iv**		24/iv		24/v
4 eggs	**8/ii**	**12/ii**	13/iv	**19/iv**	25/iv	13/v	25/v
1 egg missing	15/ii						11/vi
4 eggs missing		19/ii			13/v		
1 chick (3 or 2 eggs)	3/iii[1]		9/v	21/iv			19/vi
2 chicks (2 or 1 eggs)			10/v				20/vi
3 chicks (1 or 0 egg)			10/v			4/vi	
1 chick 0 egg				22/iv			22/vi
empty	8/iii[2]		11/v[2]	23/iv		5/vi	22/vi
No. of eggs hatched	1	0	3	4	0	4	3
1st chick flying	4/iv		14/vi	[2/vi ?]		..	21/vii
chicks last seen	27/iv		24/vi	[2/vi ?]	..	2/vii	22/vii
No. flying	1	..	2	[1 ?]	..	0	1
parents last seen	..		29/vi	[2/vi ?]	..	7/vii	22/vii

Note : Bold face indicates date nest found.
[1]—helped out of shell (see Jayakar & Spurway 1965).
[2]—unhatched eggs collected.



Area kept under observation from the roof of our house.

The house is closely hatched in the figure. Widely hatched portions indicate tarred roads. Other pairs of parallel lines indicate untarred roads or public areas bordering roads. Nests are indicated by numbered dots. Approximate maximum boundaries of territories shown by broken lines as follows : — — — — pair 3 ; ---------- pair 6 ;

•••••••••• pair 7 ; —•—•—•— pair 5.

Pairs 3 and 6 laid two clutches each: 3 and 3′, and 6 and 6′ respectively. On 6/iii, pair 3 led their only hatchling of clutch 3 away from the nest leaving 2 unhatched eggs. On 4/iv, they were first recorded nest-building and copulating in the region where they laid clutch 3′, and one or both of them were seen in this area on several days between then and the finding of the nest. We can presume that the first egg of clutch 3′ was laid on 9/iv or 10/iv. Therefore this pair, who were rearing a first brood, selected a new nest site about 29 days after they had deserted their first nest, and laid the first egg of their second clutch 5 to 6 days later. Pair 6 lost their first clutch completely on 13/v, and within 2 days, on 15/v, they were nest-building on their new site, and they also laid the first egg of their second clutch 6 days after site selection.

All seven clutches contained 4 eggs. Pair 3 were incubating before the fourth egg of clutch 3′ was laid; and pair 6 incubated their first clutch from the laying of the first egg. Indeed they often sat on the nest on 20/iv while nest-building by flicking pebbles. They were not watched during the hotter and therefore critical hours while clutch 6′ was still incomplete. Both clutches we observed through their laying (clutches 6 and 6′) took 5 days to lay, the last egg being 4 days younger than the first, and it seems a rule that birds, unlike reptiles, lay not more than one egg a day. On both occasions where all four eggs hatched (clutches 5 and 7) the whole clutch hatched in approximately 24 hours. In nest 1 in 1963, where the process was watched in detail, the fourth egg-shell was removed from the nest 23 hours 10 min. after the first. The timing of the *three* hatches of nest 6′ seems abnormally long, but even so it is one day shorter than the laying period of the full clutch of four. Therefore some regulation seems to occur causing the eggs to hatch approximately simultaneously so intra-litter selection need not be invariably biased in favour of the first hatched. Considering the early afternoon temperatures to which the nests of *V. malabaricus* are exposed, it is not surprising that incubation is not delayed until the clutch is complete. Such delay is the device used by birds nesting in cooler microclimates to obtain synchronisation of hatching. One is reminded of the observation that the litters of ' live-bearing ' fish (Poeciliidae) consist of fry which are all born at the same developmental stage though the individual embryonic lives range from 3 to 4 weeks (Turner 1937).

We have no undepleted clutch from which to calculate the incubation period defined as the interval between the first oviposition and the first hatch. Using this measure on depleted clutch 6′ we obtain 29 days. Considering the *last* oviposition to the *last* hatch we obtain 27 and 28 days from the depleted clutches 3′ and 6′ respectively. If we are correct that nest 7 was not established on 8/v, the first egg could not have been laid earlier than 9/v, and therefore the incubation period was as short as 26 days.

Considering these figures we can discuss the fact that clutch 7 was laid in the same scrape as nest 4. Unfortunately we did not learn to recognize pair 4 morphologically. Wynne-Edwards (1962, pp. 156 and 408) gives references to the re-use of a scrape during a series of seasons by different individuals of the same species, or by different species, and we do not yet know for this species how complete the re-apportioning of territories can be within one breeding season. A territory containing this scrape would be expected to extend into gardens which are invisible from our roof, as the territory of pair 7 was later seen to do. Therefore it is possible that pair 4 built a nest in one of these between 19/ii and 13/v, meanwhile relaxing its hold on the north-western part of its territory which was temporarily taken over by pair 6. Certainly birds were repeatedly seen in this area screaming at inter-specific intruders and displaying at the other conspecific pairs. However pair 6 and 7, who both finally held territories to the east of that of pair 3, were not recognized morphologically until they were associated with their respective nest sites. Using the times obtained from the other nests it is chronologically possible for pair 4 to have built a nest (4′) where it could not be seen by us, from which the young were reared, and that nest 7 represents nest 4″. There were no flying young birds seen accompanying pair 7 in the manner that the survivor of their first clutch accompanied pair 3 for more than half the incubation period of their second clutch (see next section). However, it is possible that the young may sometimes leave their parents as soon as they can fly, or the hypothesised brood 4′ may have been lost late in childhood.

The hatching success for 1964 is 15 out of 28, and if we add our two 1963 nests in which all the eight eggs hatched 23 out of 36, i.e. so far, it lies between 54 and 64%. In these estimates we make one logically dubious assumption which is probably biologically correct. The earlier hatchlings certainly step off the nest before all the eggs are hatched. Therefore, if an egg disappears before hatching has begun, we consider that egg lost (we have seen one taken by a crow, *Corvus macrorhynchos*), but if an egg disappears after hatching has begun, we assume a successful hatch, the shell having been removed and the chick having left the nest. Though our only unhatched eggs occurred in nests we were watching, we do not think this is because we minimised predation of the nest.

We are only certain that 4 of our hatchlings survived to fly, on two occasions 32 days after it, or its eldest sibling, hatched. It is probable that one chick of family 5 also survived, but this family was only recognized by its territory which was far away. Also, it is just possible that family 7 moved to a region of their territory not visible from our roof before any of clutch 7 were able to fly. That only 5 young from 28 eggs, laid by 8 or 10 parents, survived even infancy may not be disas-

trous in the light of the mortality rates discovered in *V. vanellus* (Lack 1954 ; Haldane 1955).

The Plate shows, outlined with various broken lines, the areas on which a given pair was seen feeding at any time during the season. We consider that these feeding areas coincide with the territories. Firstly, at any given instant they were mutually exclusive but contiguous, there being no neutral ground between them. Had there been a neutral ground between territories, at no place would more than one pair display, which was certainly commonly seen. No adult intruder, if noticed, was ever allowed to forage, but was greeted with agonistic behaviour, which was often followed by copulation by the pair in possession. These displays against intruders occurred not only at the boundaries between two territories but well within them. During our continuous watching in February we saw in detail many examples of the latter. If these were attempts by newcomers to appropriate some of the territory held by pair 3 in our garden they were unsuccessful. However pair 6 did move in on some of the territory previously held by 3 in the wasteland. The territory of 3 was at its largest early in the season, the pair staking a claim exceptionally early according to all previous authors. However this territory did not constantly contract but its boundaries fluctuated, perhaps even from day to day, according to whether pair 3 or pair 6 were occupied, for example with incubation, in a region remote from the disputed area. From the map, pair 7 appears to have similarly invaded part of the territory of pair 6. However as clutches 4 and 7 were laid in the same scrape, they may well have been laid by the same parents (see above). On this interpretation the relevant area was first held by pair 4 who relaxed their hold for a while and subsequently re-established it.

Secondly, the nests were also in these feeding territories. Nest 3′ was certainly in the area held while nest 3 was being incubated, and nest 6′ probably in the area associated with nest 6.

Finally, no chick too young to fly was ever seen feeding outside the territory held by its parents, and this was exceptional even after they did fly.

The maximum areas of territories 3 and 6 as shown in the map were 3.47 hectares (8.75 acres) and 2.59 hectares (6.40 acres) respectively. These are much larger than those of the European lapwing *V. vanellus* which range from 0.5 to around 2 acres. This is correlated with the different economy of *V. vanellus* where both the adults and the chicks feed outside their territories. These are only exceptionally adjoining, and at a period when *V. vanellus* was considered a common species, several frequencies ranging from 2 to 3 pairs to 18 pairs per 1000 acres were found on different habitats (Nicholson 1951, p. 77, and Wynne-Edwards 1962 for summaries), compared with the 5 (or 4) pairs of *V. malabaricus* we observed in an area of about 40 acres.

Member of a First Brood accompanying its Parents during Incubation of a Second Brood

After leaving nest 3, and before we found their second clutch (nest 3′), the parents were regularly seen with their chick in their territory during the 1½ or 2 hours before dusk while S.D.J. was making another set of observations from the roof. They were seen on all days when they were looked for, except two, and were seen to copulate three times. It is possible that they had a daily routine of movements within their territory, since on 9 days we saw them in our garden, or the garden to the west, at dusk, having just arrived there from the wasteland to the north. The solitary chick was always seen in the company of its parents until 7/iv, 3 days after it was first seen to fly, and even after that, it could frequently be found with one or other of them. This remained true on and after 12/iv when we discovered nest 3′ with three eggs already present. The chick was seen often enough during the inspections of nest 3′ for us to presume that it still spent a large part of its time in the company of its parents, and this was confirmed during our periods of continuous observation begun on 26/iv. During these periods on 26/iv and 27/iv, the chick groomed and fed in regions of shade near the new nest including the so-called tap-region which had so much valence for the incubating birds (see next section).

At this time the young bird was only a little smaller than an adult, and the black of its head and the yellow of its legs and wattles were paler. The wattles were not fully grown and did not overlap over the beak and forehead. The back was brindled instead of a uniform fawn.

When watching was continuous, it was observed that both parents pecked, lunged, flew, or ran a few steps at the chick, causing it to retreat. The chick also avoided walking too near to its parents, making detours to avoid passing within 40-50 cm. of either of them. Finally at 14.56 on 27/iv the father flew over the chick causing it also to fly. After both had landed the father performed, for a second or so, the display which a pair use, often together, at a conspecific intruder in their territory. This is derived from a ground pecking movement and quite characteristic and conspicuous, being highly ritualized. The father then ran a few steps after the chick. They paused 1.25 m. apart ; then the chick walked east into the next (the observers') garden and spent about an hour eating, grooming, sitting, and stretching. After flying away, it did not return to its family or to their territory at least until it had further developed so as to have become unrecognizable. This breaking of filial ties, like several other crises in the lives of this species (Jayakar & Spurway 1965, and next section) coincided with a severe storm from 19.30-20.30 the same evening (27/iv). It is not known whether this storm played any part in disrupting the family, nor whether the ritualized display was

more potent than the several pecks in driving off the young bird, who had spent over 17 days in the company of its parents after they had started incubating a second clutch.

As the whole of the first clutch of pair 6 was lost, there were no half-grown birds to accompany their parents during the incubation of clutch 6′. Lack (1954, p. 95) considers that pairs of *V. vanellus* never rear more than one brood a year.

Egg-wetting by pair 3

Owing to details of cultivation, we were unable to find in either garden, a viewing point acceptable to the birds, from which we could see enough to justify continuous watching of the second nest (3′) of pair 3. However as this nest was located in the same general region as nest 1 in 1963 and incubated even later in the season, it provided an opportunity to see whether birds who had not wetted their eggs during February and March would do so during April and May. Therefore, beginning just after noon on 26/iv, the tap at which pair 1 had wetted themselves before going to the nest was watched during the hottest hours of the day from the same verandah as had been used previously to watch the earlier nesting behaviour of pair 3 (Jayakar & Spurway 1965).

This tap, which is 23 metres from the south hedge of the garden immediately to the west of ours and 5.5 metres west of the hedge between them, is carried on a vertical concrete post on the west edge of a concrete pavement 1.25 m. square surrounded by a rim about 10 cm. high. The pavement slopes towards a drain in the east side near its south-east corner. As the tap dripped continuously, this drain stimulated a dense growth of small herbs just east of the rim obstructing observation of that region of the pavement in which there was always standing water.

Among these herbs grows a banana. The *Duranta* sp. hedge to the east of the tap is fortunately thin in this region, but nevertheless, during the period of observation, there was little unshaded ground between it and the banana. The region of the above-listed objects will be called the tap-region. During the periods of observation, the birds seldom left this tap-region during their off-duty periods, as we have called the period between stepping *off* and stepping *onto* the nest, and which we will discuss in detail elsewhere. The birds seldom walked through any of the regions of shade of eddies which had been their favourites while off duty from their earlier nest, and never behaved as though these had any valence for them.

Except on 26/iv, watching was always begun before 11.00 and except on 10/v and 11/v continued until 16.30. On 10/v watching was discontinued at 16.01 because the light was too poor to see the birds both of whom were rushing about and screaming. A violent dust storm began

at 16.06 followed by heavy rain at 16.08. This storm may have precipitated the desertion of the nest, and certainly introduced a doubt as to when this occurred. After the female left the tap pavement at 15.19, and the male left the nest at 15.46, neither bird was seen either to enter the tap-region or incubate again, though both parents not only flew but ran about screaming when three chicks and a sterile egg were observed in the nest at 17.10. On 11/v, as the family had not visited either the nest or the tap pavement that day, and as the chicks had walked out of the observers' field of vision before 13.49, watching was discontinued at 15.05. As 11/v was thus outside the incubation period the hours of watching are not included in Table IV.

The nest itself was obscured by the hedge, and during the middle of the day, the high sun flattered the animals' disruptive coloration making them almost invisible. But when the sun was lower, both in the morning and evening, the sitting bird was more conspicuous. However on all but 4 occasions the bird walked directly from the tap to the nest, so when the bird left the tap it was an indication that a take-over was imminent and this could be watched for. We therefore obtained timings of the duty periods but have not been able to add to our previous notes on the behaviour of the bird on duty on or around the nest.

A bird was always present on the nest when watching was begun (except on 11/v), but on 8 occasions, including 10/v, the nest was uncovered when watching ceased.

During these observation periods, the female was seen to take over incubation on 43 occasions and the male on 42 occasions. During any one observation period the number of times the two sexes assume duty cannot differ by more than one, because these alternate, but though the difference between the totals for the two sexes will be thus reduced, the virtual equality observed is more than a tautology.

When a bird was relieved from nest 3′, on all but 10 occasions (including the 3 last on 10/v and 5 others at the end of the watching period) it approached the tap usually at a brisk walking pace, but in strong sunshine it sometimes ran and jumped or stumbled over the rim of the pavement. They never flew. Once in the tap area, usually on the pavement, it groomed with high intensity usually drinking immediately on arrival. The choice of the tap and its surroundings as an off-duty resting place during a period of higher temperatures, and the introduction of repeated drinking sooner or later among the grooming movements, confirms our previous interpretation of this grooming as a method of lowering the body temperature by evaporation. The animal usually walked in and out of the tap pavement and the various regions of shade and eddies between its eastern edge and the hedge between the two gardens. The grooming gradually became more desultory as the inter-duty period progressed, but on 58 occasions the animals began to crouch on the wet

TABLE II

TIME BETWEEN LAST WETTING AND ASSUMING DUTY

minutes	<1	1	2	3	4	5	6	7	8	9	10	11	12	15	29	36	49	not timed	Total	mean	variance
♀ certain	3	10	1	1	1		3			1	1		1	2			1		25		
♀ presumed	1	2				1												1	5		
♀ Total	4	12	1	1	1	1	3	0		1	1		1	2			1	1	30	5.31	90.44
♂ certain	0	5	7	6	3	3	0	3	3	0	0	1			1	1	0		33	5.61	53.31

pavement, or in the shallow water sometimes bending forward so that their breasts as well as their bellies were wetted. Usually they walked a few steps in this position. The belly feathers were erected during these movements and the dirty water could be seen smeared on them. This *crouching* which may occur only once or may be repeated 20 times usually occurred only in the later part of an off-duty period. The exceptions were few and during the hottest periods when the animals in their hurry fell over the rim of the pavement and splashed about in the water immediately. While performing these crouches, the animals sometimes disappeared behind the plants growing by the drain often for several minutes and then walked calmly into view from behind them. At these times we have *presumed* that the birds were sitting down in the relatively deeper water behind the plants. On the five occasions when only disappearances and no crouches were recorded in off-duty periods, all for the female, we have presumed that she wet her belly, because such a sitting down would be the most efficient method of achieving this.

A belly-wetting crouch was frequently the last act performed in the tap-region before the birds stepped off the south rim of the pavement to begin the very characteristic march to the nest. The time taken for this was very variable, but it could be brisk enough to be completed in under a minute. Both birds took a rather stereotyped curved path going considerably to the west of the straight line between the tap and the nest. Table II gives the distributions of the time between the last crouch, or failing this the last reappearance from the drain region, and the time at which the bird stepped onto the nest. From this table can be seen how few were the occasions when the period between the wetting and the assumption of duty was so long that it was doubtful if the bird was wet when it took over the nest.

No differences were observed between the frequencies with which the male and the female wet their bellies either as the incubation period advanced, or as the ground or air temperatures rose, or at different hours of the day. Therefore, in Tables III and IV, the figures for the two sexes are added together. The figures are arranged in Table III according to ascending values of ground temperatures. These were taken so as to be as similar as possible to those to which the nest was exposed. The maximum air temperatures and the humidities (at some time between 08.00 and 10.00) being collected for another purpose were taken indoors in a non-airtight and frequently opened cupboard. These are thus only correlated with the conditions surrounding the eggs, though it should be stressed that in the tropics the interiors of non-airconditioned houses are much more open and ventilated than in temperate climates. From this table it is clear that the frequency of belly-wetting, and therefore egg-wetting, increases with rise in temperature. This is confirmed by Table IV in which the data are rearranged according to the hours of

TABLE III

Temperature °C.		humidity indoors	date	watching time		Assumptions of duty				
Ground	Max. indoors					♀	♂	after wetting	without wetting	proportion after wetting
				hrs.	min.					
44.5	33.5	74	28/iv	5	31	2	3	3	2	.6
49	31.5	74	26/iv	4	12	1	1	0	2	0
50.5	33	77	29/iv	6		2	2	3	1	.75
52	33.5	71	7/v	6		3	3	5	1	.83
53	32.5	74	27/iv	5	58	1	1	2	0	1.0
54	35	73	6/v	6		3	3	5	1	.83
55.5	33.5	77	30/iv	5	39	2	2	1	3	.25
56	34.5	71	2/v	6		3	3	4	2	.67
56	34	68	3/v	6		3	2	1	4	.2
57	35	73.5	4/v	6		3	3	4	2	.67
57	34.5	68	5/v	5	57	3	2	4	1	.8
57.5	34.5	71	1/v	6		3	2	5	0	1.0
58	34.5	74	9/v	6		5	4	8	1	.89
58	35.5	77	10/v	5	26	6	7	11	2	.85
60	33.5	75	8/v	6		3	4	7	0	1.0
			Total..	86	43	43	42	63	22	
47.5	35.5	72.75	11/v	4	33	0	0	0	0	..

TABLE IV

hour of day	time watched 26/iv—10/v		Change-overs				
	hrs.	min.	♀	♂	with wetting	without wetting	wetting / Total
10.30—	13	03	6	5	5	6	.45
11.30—	14	12	7	9	12	4	.75
12.30—	15		9	7	12	4	.75
13.30—	15		7	8	14	1	.93
14.30—	15		10	6	14	2	.875
15.30—	14	28	4	7	6	5	.55
Total	86	43	43	42	63	22	

the day showing that the frequency has a peak during the period just after noon.

To sum up : pair 3 who did not damp their first clutch of eggs early in the season repeatedly damped their second clutch produced when the season was more advanced and the weather was, on the whole, hotter. However the relationship between the temperature and egg-wetting is not simple. Though, during the incubation of clutch 3, 54°C. was the highest ground temperature recorded, on no fewer than 21 days out of the 28 days during which this nest was watched temperatures of 44.5°C. and higher were recorded. As the eggs of clutch 3′ were damped at these temperatures this behaviour cannot be a direct response to a ground temperature above a critical value.

In 1963 the female of pair 1 damped her feathers twice within the hour following the removal of the last egg-shell from the nest, but not subsequently. The young, who were still in the nest, were not seen to suck them. It is possible that this continuation of damping after all the eggs were hatched was a lag persisting during the shift to behaviour appropriate to the chick-shepherding stage of parental activities and may be compared with the observation that the last time a parent stepped off nest 3, this was accompanied by nest-building (Jayakar & Spurway 1965). After they deserted nest 3′, neither parent was seen to approach the tap or perform any action in the tap-region, thus suggesting that none of its previous valence remained. This desertion of both sites simultaneously, which probably occurred on the late afternoon of 10/v, was quite complete by the morning of 11/v when the parents and three chicks were observed many times before systematic observation was begun. There was no parental reaction when the unhatched egg was collected at 14.00. However this observation that belly-damping ceases at nest desertion, feathers not being used to carry water to the young birds as in *Pterocles* spp. (Marchant 1961, 1962) is not as definitive as could be wished, because the storm on the evening of 10/v had caused a considerable drop in the temperatures on 11/v (Table III). It is still possible therefore that water for drinking would be carried to the young at higher circumambient temperatures. It is also possible that the temperature thresholds for watering mobile chicks that can, and do, seek shade might be higher than that for damping stationary exposed eggs.

In our previous paper we discussed comparable behaviour in other species. We have since discovered two other descriptions, both of behaviour much more similar to that here described, and both occurring in species which Bock (1958) now includes in the genus *Vanellus* with *malabaricus*, which he considers, incorrectly, to be an African species. Owing to the kindness of Rev. W. Serle, we have read his account (1939) of a colony of *Xiphidiopterus albiceps* in Northern Nigeria cooling their eggs by wetting their underparts. Crossley (*in litt.*) observed individuals of *Hoplopterus spinosus* performing the same action in July 1952